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Holocene fluctuations in human population demonstrate repeated links to food production and climate

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We consider the long-term relationship between human demography, food production and Holocene climate via an archaeological radiocarbon date series of unprecedented sampling density and detail. There is striking consistency in the inferred human population dynamics across different regions of Britain and Ireland during the middle and later Holocene. Major cross-regional population downturns in population coincide with episodes of more abrupt change in north Atlantic climate and witness societal responses in food procurement as visible in directly dated plants and animals, often with moves towards hardier cereals, increased pastoralism and/or gathered resources. For the Neolithic, this evidence questions existing models of wholly endogenous demographic boom-bust. For the wider Holocene, it demonstrates that climate-related disruptions have been quasi-periodic drivers of societal and subsistence change.

radiocarbon | archaeology | Britain | Ireland

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Introduction

The relationship between human population dynamics, crises in food production and rapid climate change is a pressing modern concern in considerable need of higher resolution, chronologically-longitudinal perspectives. We have collected a large series of radiocarbon dates from archaeological sites in Britain and Ireland, which is a globally unique region for (a) its high density of archaeological radiocarbon sampling, (b) its unusually high proportion of well-identified botanical and faunal material and (c) its balance of dates from both research projects and rescue archaeology. For the first time, this high-resolution evidence can be considered over four different geographic regions and a broad Holocene timespan as a proxy for human demographic variability and subsistence response. We identify several episodes of regionally-consistent population decline – the later 4th millennium BCE, the early 1st millennium BCE and the 13th-15th century CE respectively – that also appear associated with episodes of rapid Holocene climate change towards more unstable, cooler-wetter conditions. We also demonstrate the existence of structured responses to these changes in the form of altered human food production strategies. The most obvious such episodes during the middle and later Holocene are likely consistent with altered north Atlantic storm regimes, reduced solar insolation and climate-related cultural and demographic impacts across north-western Europe.

Archaeological radiocarbon dates typically come from samples of bone, charred or waterlogged wood and seeds that are taken in order to date specific stratigraphic events in the surviving archaeological record. When considered in large-scale aggregate however, they also provide an anthropogenic signal of changing overall levels of past human activity and ultimately population. Some commentators highlight taphonomic and investigative biases in this record, but there is increasing agreement that, if these biases are controlled for and if the number of available dates is sufficiently high, an important demographic signal remains (see Materials and Methods). While in many areas of the world, the anthropogenic radiocarbon record is insufficient to support such aggregate treatment, in Britain and Ireland there is a long well-resourced tradition of sampling, both from active-mode academic research and responsive-mode, development-led archaeology. Furthermore, parts of Britain and Ireland lie towards the perceived margins of effective European-type agriculture and thereby can offer many of the same insights on middle and later Holocene population stability, climate change and food production as other north Atlantic Islands (Greenland, Iceland), but for a much longer and larger history of human settlement. We have therefore gathered over 30,000 existing archaeological dates from British and Irish databases, publications and grey literature reports, while also recording information about sample provenance, context and material/species (**figure 1**). The changing intensity of this anthropogenic radiocarbon record through time can be modelled via summation of the post-calibration probability distributions of individual dates (see Materials and Methods).

Results and Discussion

Looking at the overall summed distribution (**figure 1C**), there is a dramatic upswing in radiocarbon dates ca.4000-3850 BCE that coincides closely with the first arrival of Early Neolithic cereal agriculture in Britain and Ireland. Although caution is required in inferring actual population growth rates directly from rates-of-change in summed radiocarbon, the latter values exceed 1% during this earliest phase, are unlikely to be explained by increased fertility amongst farming groups alone and must in part therefore be due to migrant farmers from the European mainland, a conclusion that is consistent with current archaeo-

Significance

The relationship between human population, food production and climate change is a pressing concern in need of high-resolution, long-term perspectives. Archaeological radiocarbon dates have increasingly been used to reconstruct past population dynamics, and Britain and Ireland provide both radiocarbon sampling densities and species-level sample identifications that are globally unrivalled. We use this evidence to demonstrate multiple instances of human population downturn over the Holocene that coincide with periodic episodes of reduced solar activity and climate reorganisation as well as societal responses in terms of altered food procurement strategies.

Reserved for Publication Footnotes

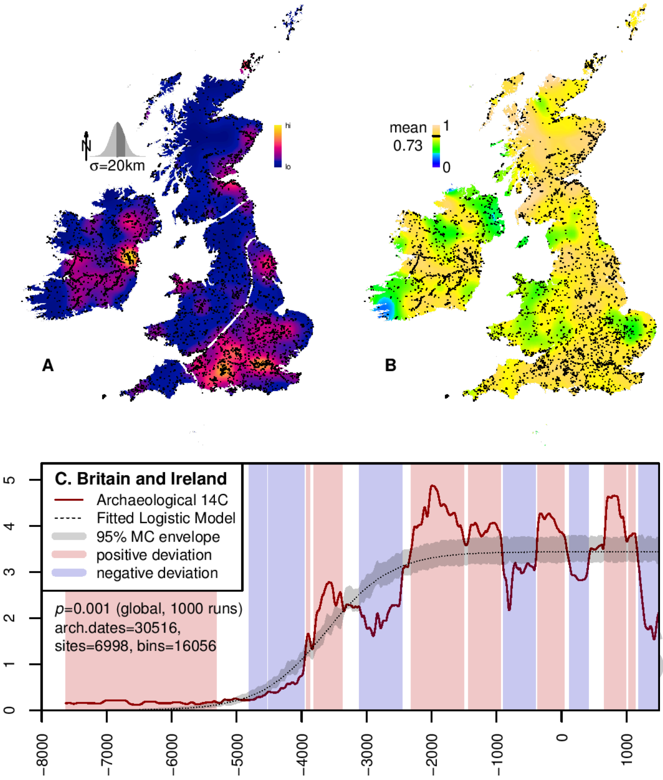

Fig. 1. (A) The kernel-smoothed intensity of archaeological radiocarbon dates from Britain and Ireland showing uneven spatial sampling (the sub-regions used in figure 2 are marked with white borders), (B) the proportion of dated samples with genus or species level identifications, (C) a summed probability distribution of all dates compared with a 95% Monte-Carlo envelope of equivalent random samples drawn from a fitted logistic model of population growth and plateau.

logical and genetic evidence (1,2). After this Early Neolithic peak, there follows decline ca.3500-3000 BCE and continued moderate downturn thereafter. This is followed by slow Late Neolithic and Early Bronze Age recovery up to a new peak ~2000 BCE, again for which there is a strong isotopic and genetic argument in favour of significant population replacement by groups from continental Europe (2,3,4). After ~1000 BCE (the last part of the Bronze Age), there is then another striking decline and, while a higher uncertainty in the calibration curve at this point inhibits precise characterisation of timing and duration, substantial recovery is only visible again by ~400 BCE. The Roman period exhibits a trough in the aggregate radiocarbon time series that is unlikely to represent a valid picture in England and Wales due to a far weaker tradition of dating Roman sites via radiocarbon (where pottery and coinage is typically used for dating instead, over the period ~50-400 CE), but may well be valid in Scotland and Ireland (see below and Supplementary Information 2). After the Roman period, there is evidence for sustained early Medieval growth, followed by an abrupt decline approximately consistent with the demographic collapse surrounding the historically well-documented episodes of the Great Famine and Black Death (~1270-1450 CE).

This radiocarbon record can be further disaggregated into sub-regions (following commonly proposed divisions, 5) to consider local consistency with, or departure from, the pan-regional pattern (**figure 2**). Restricting comparison to the post-Mesolithic period where dynamics are more abrupt, north-west England/Wales versus Scotland exhibits the highest pairwise correlation (with the range among all regional pairs being r=0.69-0.86), while Ireland exhibits more volatile dynamics than the

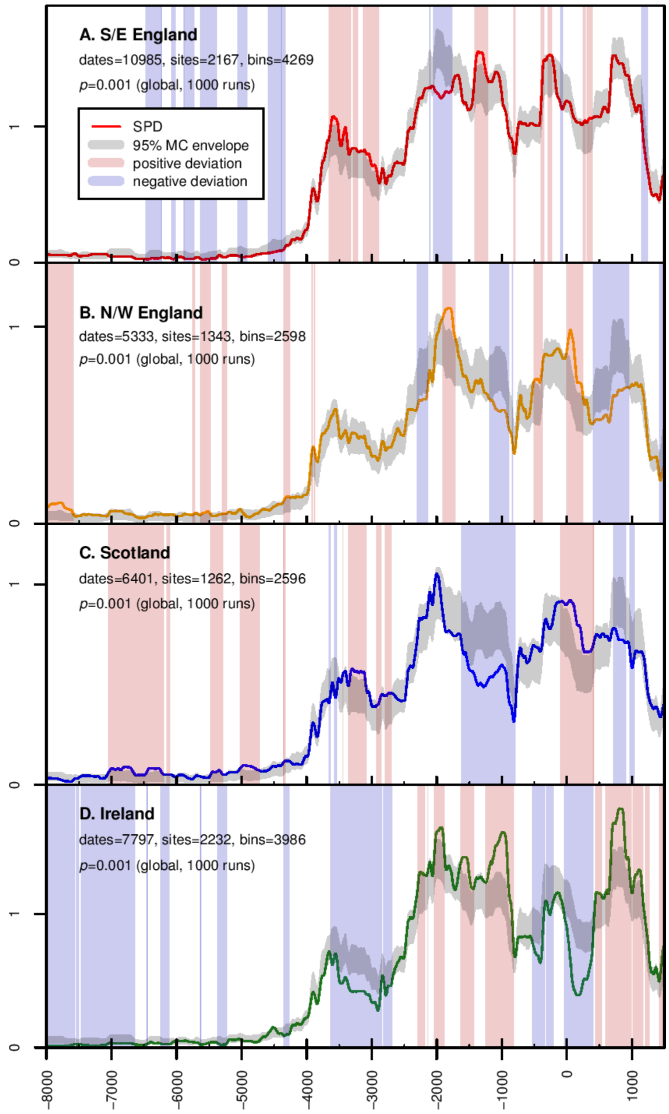

Fig. 2. Regional summed probability distributions – for (A) south-east England, (B) northern/western England and Wales, (C) Scotland and (D) Ireland – compared with a 95% Monte Carlo envelope produced by permutation of each date's regional membership.

others (CV=0.52, with the range of the other three being 0.39-0.42). In addition, the specific local radiocarbon trends exhibited by a given region in excess or deficit of the cross-regional pattern typically match very well with that region's known archaeological record, such as the very reduced archaeological evidence from Ireland in the Roman period ~1-400 CE and then sharper than average upward Irish growth ~400-800 CE in a period of both peak, archaeologically-observed settlement activity and historically-documented Irish monastic influence abroad (Supplementary Information 2). However, it is striking that all four chosen sub-regions show the same sharp Early Neolithic demographic peak ~4000-3500 BCE then decline, the same peak at the beginning of the Bronze Age ~2000 BCE, Late Bronze Age decline ~1000-800 BCE, a subsequent peak in the Late Iron Age ~250 BCE and then decline in the later Medieval period ~1250 CE at the end of the sequence. The particular cross-regional consistency at these points in the overall time series suggests an exogenous factor of some kind.

Evidence for an Early Neolithic boom-and-bust in the British Isles has already been noted by previous research, alongside

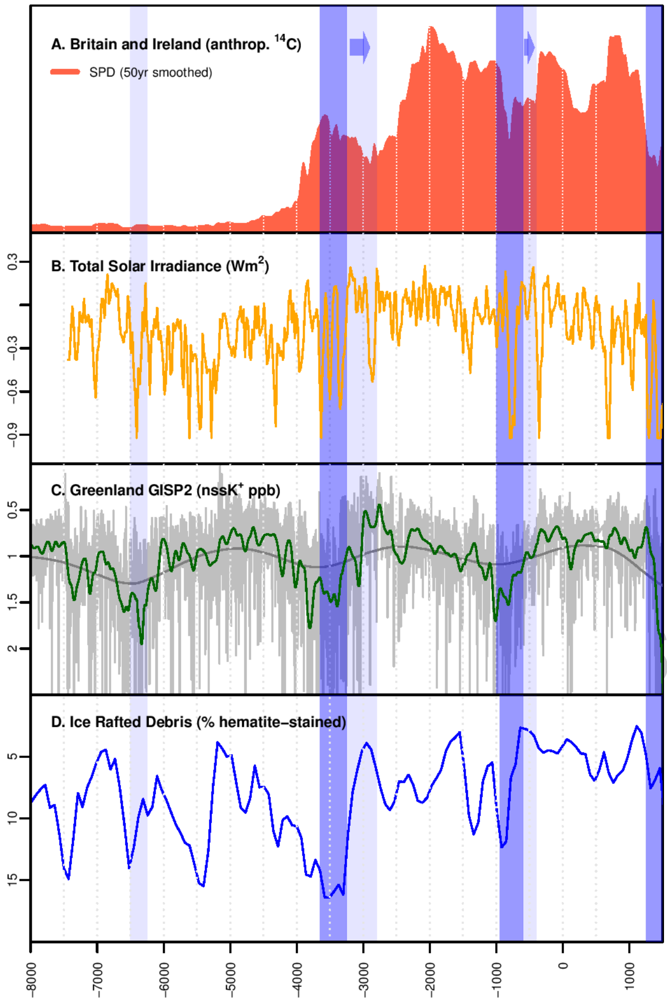

Fig. 3. Radiocarbon-inferred population and North Atlantic climate proxies: (A) aggregate anthropogenic radiocarbon dates from Britain and Ireland (as figure 1C, y-axis is linear), (B) total solar irradiance (12), (C) GISP2 potassium ion density (note descending axis, [17]), and (D) North Atlantic ice rafted debris (note descending axis, 19). Shaded blue zones indicate suggested onset and further duration of cold-wet episodes with the first one, the well-known "8.2kyr" event prior to the Neolithic and not addressed directly here.

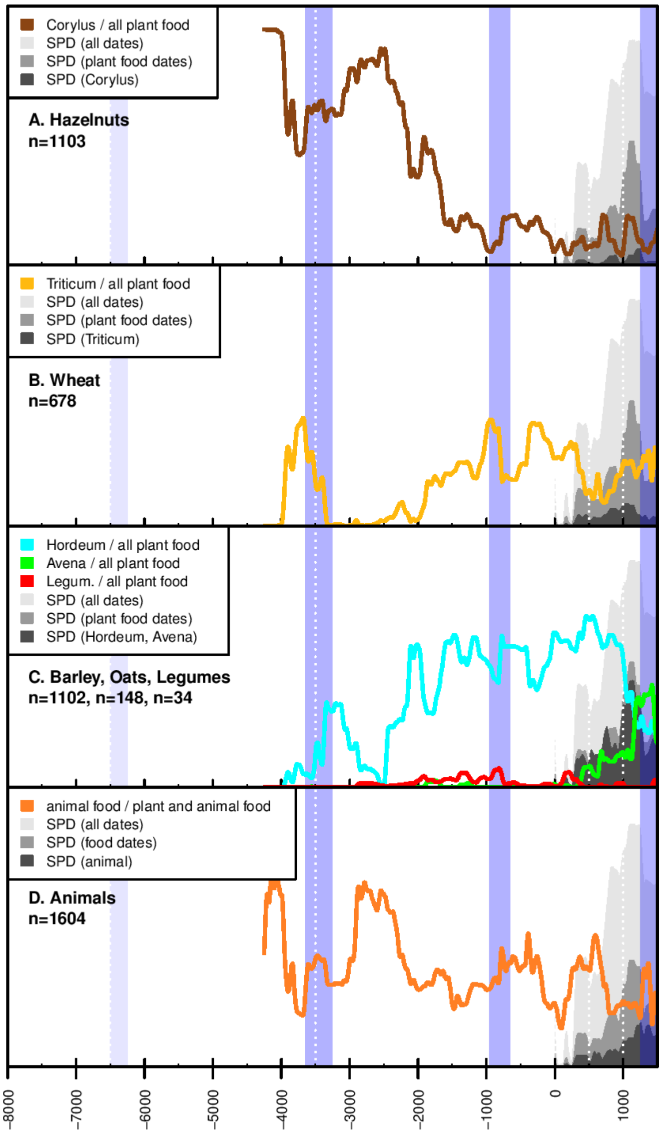

Fig. 4. The changing relative importance of major food sources across Britain and Ireland as visible in food samples directly dated for radiocarbon: (A) hazelnuts, (B) wheat (undifferentiated by species), (C) barley, oats and legumes, and (D) animals (those regularly used food sources). The coloured lines are calculated as the proportions (only calculated from ∼4250 BCE onwards due to small sample sizes prior to this). Ordinary summed probability distributions are shown in the grey (y-axes are all rescaled 0-1 for easier comparison) and an accompanying permutation tests are provided in figures SI6-SI7.

explanations stressing a collapse due either to ecological overreach by incoming farmers or the abandonment of cereal agriculture in response to declining climate conditions (6-8). **Figure 3** compares the radiocarbon record with well-known climate archives and suggests that an exogenous cause is likely for all three observed episodes of cross-regional population stagnation during (a) the end of the Early Neolithic, (b) the final Bronze Age and earliest Iron Age, and (c) the late Medieval, associated with relatively rapid changes towards more unstable conditions in Britain and Ireland, as well as colder winters and wetter summers. In particular, pan-regional demographic decline in these three episodes is consistent with reduced insolation at Hallstatt-type grand solar minima (every 2100-2500 years, 9-16). They are likewise consistent with periodic episodes of increased terrestrial salt input to the Greenland ice sheet, which in historical periods has been shown to be an excellent glaciochemical indicator of stormier, winter-like conditions and the increased dominance of Atlantic westerlies (17-19). Broadly coincident, later Holocene changes are also observable in North Atlantic oceanic regimes as separately exhibited by increased ice-rafted surface debris and reduced deep-water contributions (20-22). This evidence collectively suggests quasi-periodic solar-forcing of atmospheric and oceanic circulation with wider climatic consequences, associated with accentuated Siberian Highs and Icelandic Lows. We argue that these reorganisations have repeatedly exerted downward pressure on human population in certain parts of north-western Europe as evident for three decline phases in the high-resolution British and Irish archaeological radiocarbon record. It is very probable that similarly-timed impacts were felt by human populations in less well-documented parts of Eurasia (as already partially evident for earlier episodes, 23-24), albeit with different expression in local weather patterns, varying local human response and ultimately different positive or negative consequences for local human society. An important proximate downward forcing mechanism on human population in Britain and Ireland is likely to be exacerbated food production from reduced growing degree days for cereal agriculture and increased risk of crop loss and food insecurity due to storms. However, accompanying social dislocation and intensified epidemic outbreaks are possible accompanying phenomena. By contrast, intervening episodes of climatic amelioration may have provided good conditions for population expansion in certain areas, with the broadly simultaneous Early Neolithic colonisation of southern Scandinavia, Ireland and Britain being one probable example (25).

Radiocarbon-dated plant and animal food sources further provide an unusually well-resolved time series of potential changes in British and Irish food production (**figure 4**), as long as we are careful to consider the possible confounding effects of changing human depositional practices with regard to food remains (26). Overall, the summed probability distribution of dates from starchy food plants (cereals and hazelnuts) broadly matches the demographic signal observed in the entire radiocarbon dataset, but in contrast the relative proportion of each plant type varies significantly. Hazelnuts (*Corylus avellana*), a key comestible for Mesolithic communities prior to the arrival of agriculture, dominate the starchy plant data up to ∼4000 BCE, decline in relative popularity with the earliest Neolithic, but then rebound for half a millennium or more during the Middle-Late Neolithic (∼3500-2500 BCE), before declining again (for permutation tests, see Supplementary Information 3). In contrast, wheat (*Triticum* sp.) is a high value cereal that first appears and increases sharply at the very start of the British and Irish Neolithic, and then declines equally sharply by the end of the Early Neolithic. Much later during the Bronze Age, its relative presence in the radiocarbon record grows slowly again to a peak ∼1000 BCE, before collapsing once more. Barley (*Hordeum* sp.) is a hardier cereal species which also arrives as part of the earliest farming activity and is present throughout later periods. It is less popular than wheat early on, but far more visible during the Middle-Late Neolithic period of inferred population downturn (taking the British Isles as a whole). Oats (*Avena* sp.) only appear in consequential amounts in Britain and Ireland from the Roman period but become increasingly popular in the later Medieval period, partly replacing or complementing barley as a hardier, lower-risk, lower status food for both humans and foddered animals. The use of oats or oat/barley mixes as spring-sown, back-up crops, especially after initial harvest failures is also well-known from Great Famine/Black Death era, English manorial accounts (27). Radiocarbon samples for individual food animal species are fewer and encompass a wider range of meat, hide, wool and dairying strategies not to mention different kinds of deposition. However, comparison between the proportion of animal and plant food data suggests the greater importance of animals (as wild food) prior to the Neolithic and then also their high visibility (as domesticated herds) again in the Late Neolithic and Early Bronze Age (with a focus on *Bos* and *Sus* sp.) whilst more complicated and regionally differentiated stock-keeping strategies emerge from the Middle Bronze Age onwards (Supplementary Information 3).

Although subject to changing cultural depositional practice and representing only a fraction of the wider archaeobotanical and zooarchaeologoical record, the above-described highs and lows of directly-dated food species offer a temporally high-resolution proxy for shifting food production strategies under both advantageous and deleterious climate conditions. For example, wheat has always been a higher value, potentially higher yield cereal, and often a cash crop in later periods (particularly *Triticum aestivum*). It is therefore unsurprising that the proportion of dated wheat samples grows during peak demographic episodes but declines sharply in at least two of the inferred episodes of demographic stagnation and climate downturn: Middle/Late Neolithic and Late Bronze Age/Early Iron Age. In the former episode (after ∼3500 BCE), barley takes over as a hardy alternative cereal resource during the initial phase of demographic decline/stagnation, but then gathered hazelnuts and cattle herding become dominant strategies during the later stages and as population slowly rebounds. These indicators are consistent with what we know from larger, indirectly dated bone and crop samples from environmental archaeology (Supplementary Information 3). For the latter episode (after ∼1000 BCE), changes occur over what appears to be a shorter period, but again there are proportional increases in barley, animal products and possibly hazelnuts, and overall decline in wheat. Underlying the aggregate wheat pattern however is also regional variation, with sharper wheat declines in Ireland and north/west England, for example, but actually increased wheat proportions in south-eastern England. Such gradual regional differentiation is also a clear feature of land cover and land use from the Middle Bronze Age onwards as inferred from British and Irish pollen archives (Supplementary Information 4). Contrasting patterns of wheat investment are also potentially consistent with two alternative responses to harvest failure attested in historical periods: (a) resource switching to back-up crops in some areas (or by certain social groups) but also (b) continued speculation by others on high value wheat production as wider demand for it spikes. South-eastern England would also be the area that retained the most amenable weather conditions under climate downturn. For the Late Medieval period, crop and animal sample sizes from radiocarbon dates are much lower and the radiocarbon evidence therefore more equivocal, but contemporary documentary sources point clearly to heavily adjusted plant and animal husbandry in the period 1270-1450 CE (28). They also offer an important empirical basis for causal linkages between decreased weather stability and lower temperatures, declining food supply per capita, and further lagged human consequences such as multi-year famines, human and animal epidemics, widespread cereal market speculation, labour shortages and agricultural dis-intensification, increased violent conflict and overall population decline (29). Given these linkages, it is striking that the while a naïve assumption might be that food production and resource switching strategies should have become more successful as they became more technologically sophisticated through time, the population consequences of climate downturns appear no less severe, suggesting no major enhanced resilience in later periods and indeed potentially additional demographic and subsistence risks for economically-integrated, socially-stratified and increasingly nucleated late prehistoric to Medieval societies.

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Conclusions

Through a data-intensive approach to the British and Irish radiocarbon evidence we are therefore able to provide a detailed, long-term demographic proxy for the first time, which amongst other things, demonstrates at least three regionally-consistent episodes of population downturn. While other Holocene climate changes may also have had human impacts in this region, and other European regions need not have responded in the same way, these shared episodes of demographic change match quasi-period shifts to more unstable weather regimes in the north Atlantic and well-known solar grand minima. Furthermore, each downturn across Britain and Ireland was of varying longer-term consequence, with subsistence responses such as resource-switching and food diversification that varied through time. Exogenous climatic factors appear more likely to account for these consistencies than endogenous population over-reach on its own, although both these processes may well have operated in tandem. In any case, both archaeological and historical evidence suggest that human action has always played a role in either mitigating or exacerbating climate-driven effects.

Materials and Methods

A radiocarbon date is a measurement of residual radioactivity in a sample containing carbon, with the most widely cited measurement being a 'conventional radiocarbon age' that has been corrected for carbon isotopic fractionation (30). This age has a measurement error that is typically assumed to be a Gaussian distribution. Calibrating this radiocarbon age against observed variability in atmospheric radiocarbon through time (as documented by known standards which are mostly tree-ring sequences for the Holocene [31]) produces a post-calibration probability distribution which is irregular due to the non-linear shape of the calibration curve (32). For a regional dataset of many such calibrated probability distributions, it has become commonplace to sum them, under the assumption that a large mass of probability in certain parts of this aggregate time series offers a proxy for greater overall anthropogenic activity and higher human population in that timespan (6). Concerns that certain archaeological sites or site phases have garnered disproportionate and misleading numbers of dates (e.g. because they were better resourced scientific projects) can been addressed by pooling adjacent dates from the same site and rescaling these sub-site clusters before summing distributions between different sites. In this paper, we cluster temporally uncalibrated dates from the same site that are within 100 years of each other (via a complete-linkage, agglomerative hierarchical method [33]). Date distributions falling in the same cluster are pooled and divided by the number of contributing dates in the cluster, before these pooled distributions are aggregated overall. Some software for radiocarbon date calibration normalise the post-calibration distribution of each date to ensure it sums to 1 under the curve before summing multiple dates or performing any other modelling procedure. However, this rescaling leads to not all calendar dates having equal probability of occurrence and creates abrupt spikes in the summed probability distributions at points where the calibration curve is steep (34). We have therefore chosen not to rescale the calibrated date distributions before summation, but address the methodological implications in greater detail in SI, and consider the alternative result where dates are normalised, concluding that the paper's main conclusions remain consistent in either case.

To explore the degree to which an observed summed probability distribution is well-described by a theoretical null model of demographic change, we first fit such a model (e.g. exponential, logistic, uniform) to the observed data on the calendar scale. In this case, a logistic model was preferred given the observed distributional shape and an assumption that there might be post-Neolithic, pre-Roman upper bound to population growth. The model of expected population intensity is then back-calibrated, and a set of conventional radiocarbon ages (equal to the number of observed dates) is simulated proportional to the modelled per-C14 year amplitude. These simulated dates are then calibrated and summed. Repeating this process many times (e.g. 1000) provides a global goodness-of-fit test and 95% critical envelope with which to assess local departures from the theoretical model (6,35). A second kind of test used here holds constant the date of a given sample but shuffles its label (e.g. the geographic region it comes from or the material type/species of the sample). This permutation test creates conditional random sets (e.g. 1000) and a 95% critical envelope with which to assess region-specific or species-specific departures from the global trend (33). Such a technique also addresses the challenge of reduced sample sizes (e.g. for particular plants), as the resulting envelopes are correspondingly larger in such cases.

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